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EDAPHIC AND GEOGRAPHIC ORIGINS OF VARIETAL DIFFERENTIATION IN *ERIOGONUM CALCAREUM*

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ABSTRACT

The narrowly endemic vascular plant species *Eriogonum calcareum* (S. Stokes) Grady & Reveal (Polygonaceae) is restricted to barren outcrops composed of Miocene to Pleistocene silicic volcanic ashes scattered throughout southwestern Idaho and southeastern Oregon. We hypothesize that varieties *calcareum* and *sceptrum* are morphologically, geographically, and ecologically differentiated. To test this hypothesis, we measured morphologic and edaphic parameters among 27 populations of *E. calcareum* across the range of the species. *Eriogonum calcareum* var. *calcareum* ranges from eastern Malheur County, Oregon, to southwestern Washington and Payette counties, Idaho, has sessile involucres with hairs sparsely to moderately covering the tube, shorter scape lengths, and narrower leaves. *Eriogonum calcareum* var. *sceptrum* (Reveal) Reveal & Mansfield ranges from Canyon County, Idaho, southeast through Owyhee, Twin Falls, and Elmore counties, has pedunculate involucres that are glabrous to partially floccose at the distal end of the tube, longer scape lengths, and wider leaves. Although some populations have not fully differentiated, plants in the northwestern end of the range (var. *calcareum*) occupy soils significantly higher in both Mg (9.78 cmol/kg; $P < 0.001$) and K (2.84 cmol/kg; $P = 0.018$), and lower in pH (5.15; $P = 0.002$) and Ca/Mg (3.03; $P = 0.016$) than plants in the southeastern end of the range (var. *sceptrum*: Mg: 2.81 cmol/kg; K: 0.82 cmol/kg; pH: 7.82; Ca/Mg: 29.64). The morphological differentiation of the populations justifies a separation of var. *calcareum* and var. *sceptrum* despite the existence of populations with ambiguous morphologies. Population differentiation is likely driven by both geographic isolation and edaphic selection.

Key Words: edaphic, endemism, *Eriogonum*, evolution, exchangeable cations, selection, southeastern Oregon, southwestern Idaho.

Islands offer exceptional opportunities for the study of differentiation and speciation in plants (Stuessy 2006; Comes et al. 2008; Givnish 2010). Barren outcrops comprised primarily of Miocene to Pleistocene lacustrine and fluvial deposits, including beds of silicic volcanic ash, create islands of unique edaphic habitats throughout southeastern Oregon and southwestern Idaho (Swirydczuk 1977; USGS 2015). These islands of barren substrate surrounded by large expanses of shrub-steppe plant communities support many endemic vascular plant species (Table 1).

Despite the large number of species endemic to these diverse edaphic islands, few studies have investigated the relationship between the properties of the soil substrate and either the species' distributions or their evolution (Grimes 1984; Brokaw and Hufford 2010). Edaphic endemism on soils of ultramafic lithologic parentage, in contrast, has been widely investigated (Proctor and Woodell 1975; Kruckeberg 1985; Brooks 1987; Kruckeberg 2002; Brady et al. 2005; Sambatti and Rice 2007; Wright and Stanton 2007; Anacker et al. 2011; Harrison and Rajakaruna 2011; Moore et al. 2014; Escuardo et al. 2015; Medeiros et al. 2015). In particular, cation compositions vary between ultramafic and non-ultramafic soils. In ultramafic soils, unusually high concentrations of Mg, relatively low concentrations of K and Ca, relatively high pH (relative to adjacent soils), low Ca:Mg ratios, and anomalously high concentrations of other metal cation species, such as Ni, Cr, and Co, create environments that impose intense selection pressures driving adaptation (Sambatti and Rice 2006; Medeiros et al. 2015) and speciation (Brooks 1987; Taylor et al. 2002), and leading to high degrees of endemism (Harrison and Rajakaruna 2011).

The ash deposits that are intercalated throughout the lacustrine and fluvial sediments of Miocene to Pleistocene Lake Idaho and other smaller basins in southeastern Oregon and southwestern Idaho originated in separate volcanic events (Kittleman 1967; Swirydczuk 1977; Kimmel 1979; Izett 1981; Swirydczuk et al. 1982) and are consequently likely to be of differing compositions. Differences in cation composition might be expected in different ash outcrops and such differences might be expected to impose differential selection pressures on the plants inhabiting the barren edaphic outcrop islands of southwestern Idaho and southeastern Oregon. Thus, we investigated the variation among such outcrops in relation to the morphologic variation and geographic distribution in the endemic plant species *Eriogonum calcareum* (S. Stokes) Grady & Reveal.

The regionally endemic *Eriogonum calcareum*, originally described as *E. ochrocephalum* S. Watson subsp. *calcareum* S. Stokes, is restricted to the barren outcrops of the Glenns Ferry Formation to the east in Idaho and the Deer Butte and Bully Creek Formations to the west in Oregon. Both as *E.*

TABLE 1. Vascular plant species endemic to silicic volcanic ash outcrops in southwestern Idaho and southeastern Oregon (Grimes 1984; Findley 2004; Mansfield 2010). Distributions and descriptions of Sucker Creek and Bully Creek Formations are from Kittleman (1967); Deer Butte Formation from Corcoran et al. (1962); and Chalk Hills and Glenns Ferry Formations from Malde and Powers (1962), Kimmel (1979), and Swirydczuk et al. (1982). Taxonomy is consistent with Intermountain Flora (Cronquist et al. 1984; Barneby 1989; Cronquist 1994; Cronquist et al. 1997; Holmgren et al. 2005; Holmgren et al. 2012), except when taxa have been described more recently.

Outcrops	Taxa	References
Highly weathered, clay-rich Miocene deposits of the Sucker Creek Formation.		
	Cymopterus glomeratus Raf. var. *greeleyorus* (J.W. Grimes & P.L. Packard) R.L. Hartm.	Grimes and Packard 1981, George et al. 2014
	Lomatium bentonitum K.M. Carlson & Mansfield	Carlson et al. 2011
	Lomatium packardiae Cronquist	Cronquist 1992
	Mentzelia mollis M. Peck	Glad 1976
	Phacelia lutea (Hook. & Arn.) J.T. Howell var. *calva* Cronquist	Halse 1981
Lithified ash-tuff of the Leslie Gulch unit of the Sucker Creek Formation.		
	Ivesia rhypara Ertter & Reveal var. *rhypara*	Ertter and Reveal 1977
	Mentzelia packardiae Glad	Glad 1976
	Monardella angustifolia Elvin, Ertter & Mansfield	Elvin et al. 2014
	Phacelia lutea (Hook. & Arn.) J.T. Howell var. *mackenzieorum* J.W. Grimes & P.L. Packard	Grimes and Packard 1981
	Senecio ertterae T.M. Barkley	Barkley 1981
	Trifolium owyheense Gilkey	Gilkey 1956
Deer Butte, Bully Creek, Chalk Hills and/or Glenns Ferry Formation.		
	Astragalus cusickii A. Gray var. *sterilis* (Barneby) Barneby	Cronquist et al. 1989
	Astragalus nudisiliquus A. Nelson	Barneby 1964; Cronquist et al. 1989
	Chaenactis cusickii A. Gray	Cronquist 1994
	Cryptantha propria (A. Nelson & J.F. Macbr.) Payson	Cronquist et al. 1984
	Eriogonum calcareum (S. Stokes) Grady & Reveal	Reveal 1989; Reveal and Mansfield 2014
	Eriogonum chrysops Rydb.	Rydberg 1917
	Eriogonum novonudum M. Peck	Peck 1945
	Eriogonum salicornioides Gand.	Gandoger 1906
	Penstemon miser A. Gray	Gray 1886

ochrocephalum and as *E. calcareum*, two varieties—*calcareum* and *sceptrum*—have been recognized (Reveal 1989; Reveal and Mansfield 2014). However, some field botanists in Idaho question whether varietal distinction is justified by noting the existence of intermediate populations. These varieties may be similar enough as to represent two extreme forms on a continuum rather than distinct varietal forms. If they are distinct varieties, then they should have either distinct geographic distributions or distinct ecological settings or both. The purpose of this study is to investigate the morphological variation in relation to the geographical distribution and cationic composition of the soil substrate. More specifically, we test the hypothesis that the two morphologically recognized varieties, *calcareum* and *sceptrum*, are differentiated morphologically, geographically, and by their soil cation compositions, and should, thus, be recognized at the variety level.

METHODS

Morphological Characteristics

We measured four distinguishing characteristics (Reveal and Mansfield 2014)—scape length, leaf width, peduncle length, and vestiture coverage on the involucre (as defined below)—in 27 accessions of *Eriogonum calcareum* from 25 outcrops across its full geographic range represented by specimens present in the College of Idaho's Harold M. Tucker Herbarium (CIC, Table 2). Twenty-three unique outcrops were sampled, and two additional outcrops were sampled in two different years to check for inter-annual variation. Thus, accessions 11135 and 23963 are from the same outcrop in Elmore Co., and accessions 1468 and 14078 are from the same outcrop in Malheur Co. (Table 2). The longest scape, widest leaf, and longest peduncle were measured in each accession. Vestiture coverage on the involucre was measured as the ratio of the length of the involucre covered by floccose hairs to the total length of the involucre averaged for five involucres in each of two inflorescences per accession. Figure 1 illustrates these characters. Vestiture coverage data were arcsine square-root transformed before conducting statistical tests (Sokal and Rohlf 1995). Results were analyzed to determine statistical significance using the statistical software SigmaPlot 13.0 (Systat Software, Inc. San Jose, CA). Student's t-tests were used except when data were not normally distributed. In those cases, a Mann Whitney U-test was performed. Populations having all characteristics unambiguously indicating either var. *calcareum* or var. *sceptrum* are hereafter referred

TABLE 2. Specimens of *E. calcareum* used in this study. Specimens are located in the Harold M. Tucker Herbarium (CIC). Involucre vestiture coverage is defined in the Methods section. Locations and geological formation age are estimated by geo-referencing data on herbarium label. Outcrops sampled for soils are indicated.

Accession	County	Latitude	Longitude	Variety determination	Soil collection	Scape length (cm)	Leaf width (cm)	Peduncle length (mm)	Involucre vestiture coverage	Geological epoch of deposit
2988	Owyhee	42.7224	115.7959	var. *sceptrum*		40.3	0.9	1.2	0	Pliocene
24795	Owyhee	43.308	116.5801	var. *sceptrum*		25	0.7	0.5	0	Holocene
342	Owyhee	42.8006	116.0229	var. *sceptrum*		26	0.8	0.63	0	Pliocene
12642	Owyhee	42.743	115.782	var. *sceptrum*		25.5	0.7	1	0	Pliocene
17273	Owyhee	43.0609	116.4611	var. *sceptrum*	H	36.8	1.1	1	0	Pleistocene
17493	Twin Falls	42.7459	114.9175	var. *sceptrum*	CN	28	0.8	0.6	0	Early Pleistocene and Late Pliocene
1843	Twin Falls	42.7022	114.8394	var. *sceptrum*		21.5	0.5	0.8	0	Pliocene
11135	Elmore	43.0028	115.2111	var. *sceptrum*		38.5	1	1.7	0.3	Late Pleistocene
7151	Elmore	43.0028	115.2111	var. *sceptrum*		30	0.5	1.5	0.2	Late Pleistocene
23963	Elmore	43.0028	115.2111	var. *sceptrum*		26.5	0.7	1.5	0.4	Late Pleistocene
19412	Owyhee	42.8006	115.7873	var. *sceptrum*	HC	26.3	0.7	2	0	Middle Pleistocene
33786	Owyhee	42.981	116.316	var. *sceptrum*	CC	34.8	0.9	1	0	Early Pleistocene and Late Pliocene
26710	Malheur	44.1775	117.2563	var. *calcareum*	MH	16.5	0.8	0.2	0.6	Miocene
43115	Payette	44.08	116.597	var. *calcareum*	BB	16.5	0.5	0.2	0.6	Pliocene
4765	Washington	44.16	116.63	var. *calcareum*		9	0.4	0.2	0.4	Pliocene
41577	Baker	44.59	117.4	var. *calcareum*	MC	15	0.5	0	0.4	Miocene to Pliocene
41587	Baker	44.51	117.41	var. *calcareum*	MC	8	0.4	0	0.6	Miocene to Pliocene
28266	Payette	44.0742	116.5446	var. *calcareum*		15	0.6	0.2	0.7	Miocene
4769	Baker	44.5851	117.5047	var. *calcareum*		9.3	0.8	0	0.7	Miocene to Pliocene
4766	Malheur	44.2352	117.3782	var. *calcareum*		23.5	0.5	0.2	0.8	Miocene to Pliocene
14078	Malheur	43.9327	117.6587	var. *calcareum*	HW	18.5	0.5	0.1	0.7	Miocene to Pliocene
32002	Malheur	43.927	117.66	var. *calcareum* approaching var. *sceptrum*		21.5	0.7	0.1	0.5	Holocene
4768	Malheur	43.9327	117.6587	var. *calcareum* approaching var. *sceptrum*	HW	17	0.5	0.3	0.3	Miocene to Pliocene
4770	Malheur	43.9034	117.2969	var. *calcareum* approaching var. *sceptrum*		27.5	0.6	0.7	0.5	Miocene to Pliocene
12641	Twin Falls	42.6569	114.8039	var. *sceptrum* approaching var. *calcareum*		22.5	0.9	0.5	0.2	Miocene
40528	Twin Falls	42.9081	114.9839	var. *sceptrum* approaching var. *calcareum*		27	0.8	2.2	0.1	Early Pleistocene and Late Pliocene
17395	Elmore	43.0173	115.2508	var. *sceptrum* approaching var. *calcareum*	OH	18	0.5	2.2	0.6	Early Pleistocene and Late Pliocene

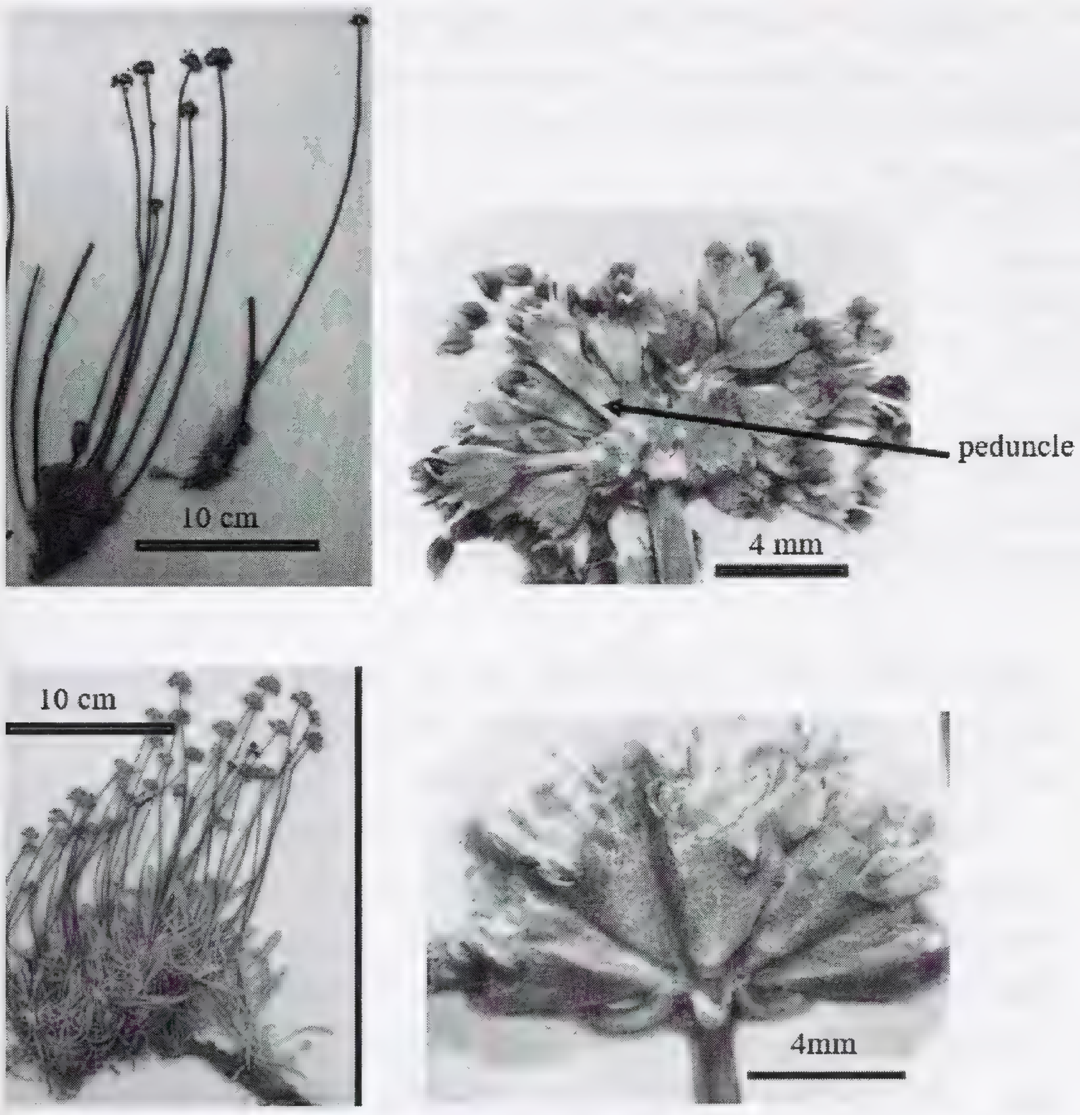

FIG. 1. Habits (left) and inflorescences (right) of 'consistent' var. *sceptrum* (top row) and 'consistent' var. *calcareum* (bottom row). Involucres of var. *sceptrum* are typically glabrous (vestiture coverage = 0 in the specimen illustrated) and on distinct peduncles; involucres of var. *calcareum* are typically quite floccose (vestiture coverage = 0.6 in the specimen illustrated) and sessile.

to as 'consistent' var. *calcareum* or 'consistent' var. *sceptrum,* respectively. In some cases, populations of otherwise 'consistent' var. *calcareum* possessed one of the characteristics typical of var. *sceptrum.* These populations are referred to as "var. *calcareum* approaching var. *sceptrum.*" Similarly, some populations with all but one characteristic typifying var. *sceptrum* are referred to as "var. *sceptrum* approaching var. *calcareum*".

Study Sites

Soil samples were collected at nine outcrops occupied by populations, which were selected to represent the full range of geographical and morphological variation (Table 2). Three of these outcrops—Manning Creek (MC), Moores Hollow (MH), and Bannister Basin (BB)—were selected because they possess populations of 'consistent' var. *calcareum.* Four sites—Crow's Nest Road (CN), Hwy 78 (H), Hot Creek Road (HC), and Castle Creek (CC)—were selected because they possess populations of 'consistent' var. *sceptrum.* Finally, two sites—Harper-Westfall (HW) and Old Hwy 30 (OH)—were chosen as areas occupied by morphologically ambiguous populations of either var. *calcareum* approaching var. *sceptrum* or var. *sceptrum* approaching var. *calcareum.* Locations are identified in Table 2.

Soil Sampling

Three soil samples were collected at each of the nine soil study sites during either the summer of 2012 or winter of 2015. At each site, samples were collected randomly from within an area of 900 m^2 (depending on outcrop size) centered in the vicinity of the highest density of *E. calcareum* plants. After collection, all samples were placed in a drying oven for approximately 24 hr at 105°C, and then ground with a mortar and pestle to break apart large clumps.

Soil Composition Analysis

Three-hundred fifty grams from each soil sample were sent to the University of Idaho's Analytical Sciences Laboratory in Parma in either October 2012 or March 2015 for analysis of soil compositional properties. Properties analyzed were pH and the extractable cations: Mg, K, Ca, and Na. The mean and standard deviation of soil properties for each study site were calculated using the statistical computing program SigmaPlot 13.0 (Systat Software, Inc. San Jose, CA). Data from 'consistent' var. *calcareum* sites were then compared to data from 'consistent' var. *sceptrum* sites to evaluate statistical significance. These data were then compared again with the inclusion of the soils from the two ambiguous populations (HW and OH).

RESULTS

Morphological Characteristics

Twenty-one of the 27 populations of *E. calcareum* were unambiguously categorized as either var. *calcareum* or var. *sceptrum* (Table 2). In six populations at least one character was ambiguous. Populations were thus placed into the groups: 'consistent' var. *calcareum* (n = 9), 'consistent' var. *sceptrum* (n = 12), var. *calcareum* approaching var. *sceptrum* (n = 3), and var. *sceptrum* approaching var. *calcareum* (n = 3). Means of all four measured characteristics differed significantly between the two 'consistent' varieties (Table 3). When data were reanalyzed after including the six ambiguous specimens, the means changed slightly, however the levels of statistical significance of difference did not change (Table 3).

Geographical Distribution

Sites containing 'consistent' var. *calcareum* were all located in the northwestern portion of the *E. calcareum* range, all north the Snake River (or west as the river turns north near the Oregon-Idaho border, Fig. 2). Alternatively, sites containing 'consistent' var. *sceptrum* were all in the southeastern range of *E. calcareum* and all south of the Snake River (or north of it within half a mile in Elmore County). Outcrops throughout much of the southern extent of the range tended to be smaller and

TABLE 3. Morphological characteristics of the two varieties of *E. calcareum.* The first two columns include only 'consistent' specimens; the third and fourth columns (all) include the addition of morphologically ambiguous specimens. Values are means (one standard deviation); significance of first three rows was assessed by Student t-tests; last row by Mann Whitney U-test. * "Involucre vestiture coverage" is defined in the Methods section.

Character/taxon	Consistent var. *sceptrum*	Consistent var. *calcareum*	All var. *sceptrum*	All var. *calcareum*	Significance
Scape length (cm)	29.92 (6.10)	14.58 (5.07)	28.47 (6.46)	16.44 (5.91)	$P < 0.001$
Leaf width (cm)	0.76 (0.19)	0.54 (0.16)	0.77 (0.18)	0.57 (0.14)	$P = 0.006$
Peduncle length (mm)	1.11 (0.48)	0.12 (0.10)	1.22 (0.60)	0.18 (0.19)	$P < 0.001$
Involucre vestiture coverage*	0.08 (0.14)	0.61 (0.14)	0.12 (0.19)	0.57 (0.15)	$P < 0.001$

occasionally did not support any populations of *E. calcareum.* Sites occupied by morphologically ambiguous populations were located at the edge of the range of the variety. That is, sites occupied by var. *calcareum* approaching var. *sceptrum* are at the southwestern edge of the var. *calcareum* range, and sites occupied by var. *sceptrum* approaching var. *calcareum* are at the northeastern edge of the var. *sceptrum* range (Fig. 2).

Soil Analyses

Outcrops occupied by 'consistent' var. *calcareum* had significantly higher levels of extractable K (mean = 2.06 cmol/kg; $P = 0.018$) and Mg (mean = 10.50 cmol/kg; $P < 0.001$) than outcrops occupied by 'consistent' var. *sceptrum* (K mean = 0.74 cmol/kg; Mg mean = 3.03 cmol/kg; Table 4). When analyses included sites occupied by all populations—that is, those with 'consistent' and ambiguous morphologies—both K and Mg concentrations remained significantly different ($P = 0.030$ and $P < 0.001$, respectively). Furthermore, when soils from all populations were analyzed, those occupied by var. *calcareum* (including those approaching var. *sceptrum*) had significantly lower Ca/Mg (mean = 3.03; $P = 0.016$) and lower pH (mean = 5.15; $P = 0.002$) than soils occupied by var. *sceptrum* (including those approaching var. calcareum, Ca/Mg mean = 29.64; pH mean = 7.82) (Table 4).

DISCUSSION

The two varieties of *E. calcareum* can be distinguished morphologically (Table 3) using the characters identified by Reveal (1989) and Reveal and Mansfield (2014). The involucres of unambiguous ('consistent') *E. calcareum* var. *sceptrum* are nearly glabrous with floccose vestiture covering only 8% of the distal portion of the tube, and they are on peduncles that are 1.11 ± 0.48 mm long. Scapes are (18-) 24–36 (-40) cm long; leaves are (0.5) 0.6–1.0 (1.1) cm wide. The involucres of unambiguous ('consistent') *E. calcareum* var. *calcareum* have floccose vestiture covering 61% of the distal portion of the involucre tubes, and the peduncles are nearly sessile (0.12 ± 0.10 mm long). Scapes are (8-) 10–20 (-24) cm long; leaves are 0.4–0.8 cm wide. The most obvious difference in the field is that mature *E. calcareum* var. *sceptrum* is a taller, more erect, narrower plant. Alternatively, var. *calcareum* appears as a more matted, broader plant (Fig. 1).

Populations with ambiguous character combinations had most morphological characteristics representative of one variety, but at least one of these characteristics was more typical of the other variety (Table 2). For example, var. *sceptrum* approaching var. *calcareum* specimens varied in the extent of vestiture on the involucres and peduncle length. That is, accession 17395 from Elmore Co. has the longer peduncle, broader leaves, taller scape, and more erect stature of var. *sceptrum*, but has the floccose distal involucre regions (vestiture coverage of 0.6) typical of var. *calcareum.* One accession from Twin Falls Co. (12641) has the short peduncle of var. *calcareum* but otherwise has the var. *sceptrum* phenotype. Two accessions from southern Malheur Co. (32002 and 2770) identified as var. *calcareum* approaching var. *sceptrum* had longer scape lengths (21.5–27.5 cm) than the 'consistent' var. *calcareum* specimens (8–23.5 cm).

Despite some ambiguity in morphological characters (Table 2), the two described varieties are completely allopatric, with var. *sceptrum* populations occurring further south and east in the range (Fig. 2). The outcrops occupied by the two varieties are comprised of sediments with differing origins (Table 2; Kittleman 1967; Swirydczuk 1977; Kimmel 1979; Izett 1981; Swirydczuk et al. 1982) and compositions (Table 4). Few studies have been conducted on the mineral compositions of these outcrops. Much of region occupied by var. *sceptrum* is in the Glenns Ferry Formation, which is comprised of lacustrine and fluvial sediments of Miocene to Pleistocene Lake Idaho (Idaho Group), including oolitic limestones (Swirydczuk 1977; Kimmel 1979; Swirydczuk et al. 1982). The region occupied by var. *calcareum* is similarly comprised of lacustrine and fluvial sediments of the Bully Creek (Kittleman 1967) and Deer Butte Formations (Corcoran et al. 1962), but being from the more western region of ancient "Lake Idaho", apparently lacks the oolitic limestone deposits due to the depth and sedimentation patterns in the ancient lake. Although 'consistent' var. *calcareum* populations occupy sediments spanning earlier geological epochs (late Miocene to early Pleistocene) than 'consistent' var. *sceptrum* populations (Pliocene to mid-Pleistocene), the age of ashes is unlikely to be

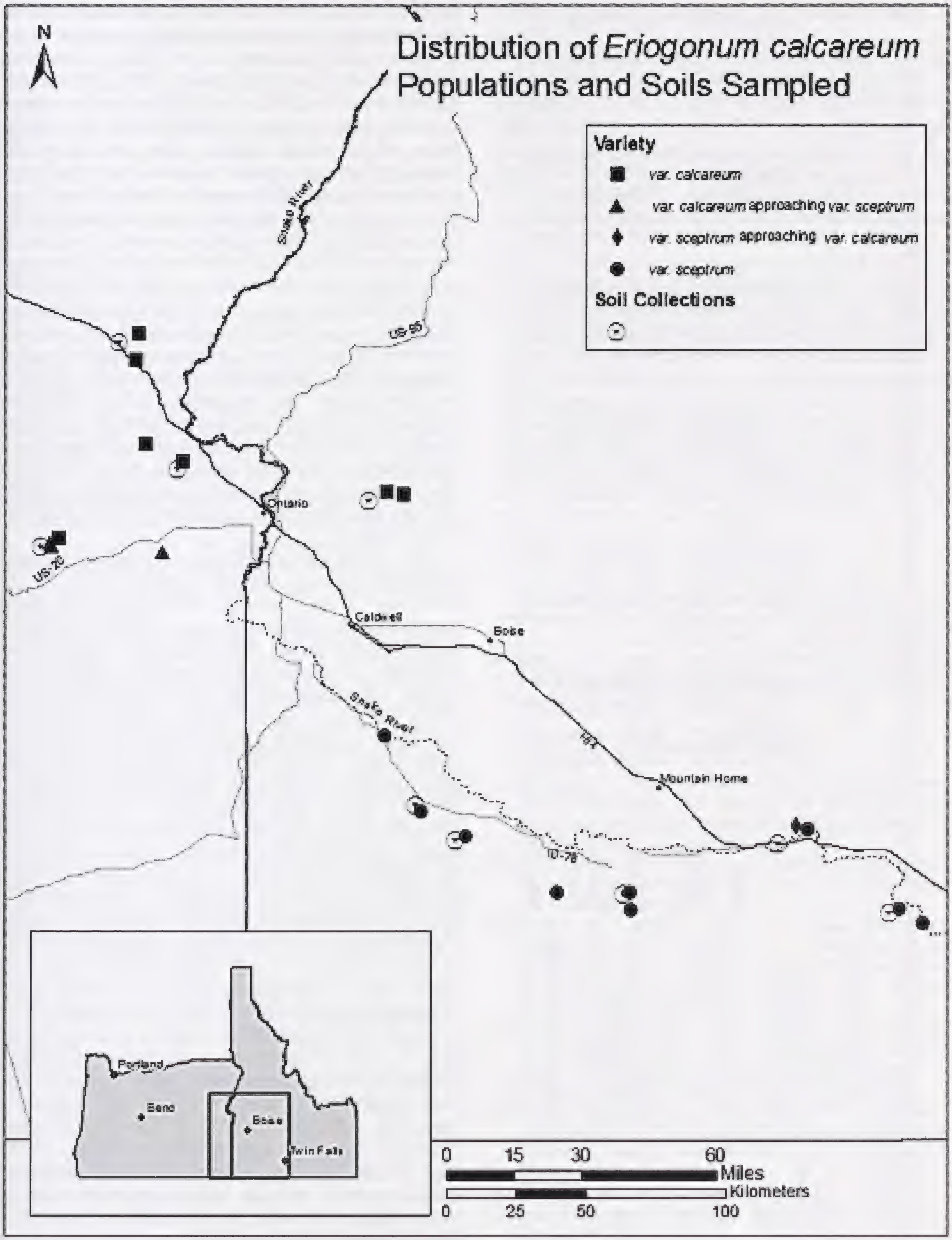

FIG. 2. Geographic locations of populations of the two varieties of *E. calcareum* and soil collection locations.

indicative of compositional differences. Populations of var. *sceptrum* occur on sites with both low Mg and low K concentrations that tend to have a slightly basic pH. Yet, the levels of Mg and K are not so low as to be in the range that normally limits plant growth (Epstein 1972). Populations of var. *calcareum* occur on sites with much higher acidity (more than 100 fold greater proton concentrations). Although

TABLE 4. Soil chemistry of the *E. calcareum* study sites. Values are means (one standard deviation); significance assessed by t-test: differences at $P < 0.05$ are denoted as "*". All extractable cations measured as cmol/kg.

	Geological epoch		Ca	K	Mg	Na	pH	Ca/Mg
Northern (var. *calcareum*)								
Manning Creek Rd (MC)	Miocene to Pliocene		20.67 (4.93)	1.33 (0.25)	9.97 (1.84)	2.73 (0.40)	6.77 (1.02)	2.18 (0.83)
Moores Hollow (MH)	Miocene to Pliocene		15.67 (4.04)	2.20 (0.35)	10.27 (4.73)	4.73 (3.00)	3.87 (0.21)	1.69 (0.52)
Bannister Basin (BB)	Pliocene		47.50 (31.44)	2.65 (0.84)	11.27 (2.74)	2.88 (1.35)	5.35 (0.30)	3.88 (1.86)
		Mean	27.94 (17.12)	2.06 (0.67)*	10.50 (0.68)*	3.45 (1.11)	5.35 (3.87)	2.58 (1.15)
Harper/Westfall (HW)	Miocene to Pliocene		34.33 (13.65)	5.17 (2.29)	7.6 (6.88)	3.10 (2.79)	4.60 (0.35)	9.85 (11.26)
		Mean All	29.54 (14.34)	2.84 (1.65)*	9.78 (1.55)*	3.36 (0.93)	5.15 (1.24)*	3.03 (1.81)*
Southern (var. *sceptrum*)								
Hwy 78 (H)	Pliocene		21.40 (15.40)	0.68 (0.59)	3.64 (3.68)	1.74 (2.83)	7.27 (0.06)	10.41 (7.83)
Castle Creek (CC)	Early Pleistocene and Late Pliocene		130.83 (100.25)	1.18 (0.08)	2.97 (0.79)	4.13 (5.36)	8.02 (0.38)	46.82 (35.91)
Hot Creek Rd (HC)	Middle Pleistocene		87.33 (58.56)	0.77 (0.04)	2.83 (0.45)	0.57 (0.08)	7.90 (0.00)	32.12 (21.64)
Crow's Nest Rd (CN)	Early Pleistocene and Late Pliocene		26.00 (0.00)	0.33 (0.08)	2.67 (0.59)	0.09 (0.00)	8.00 (0.20)	10.12 (2.51)
		Mean	66.39 (52.43)	0.74 (0.35)*	3.03 (0.43)*	1.63 (1.80)	7.95 (7.43)	24.87 (17.90)
Old Hwy 30 (OH)	Quaternary (Pleistocene)		47.33 (25.70)	1.13 (0.12)	1.93 (0.65)	0.09 (0.00)	7.90 (0.10)	29.64 (25.75)
		Mean All	62.58 (46.20)	0.82 (0.35)*	2.81 (0.61)*	1.32 (1.71)	7.82 (0.13)*	29.64 (10.27)*

the var. *calcareum*-occupied outcrops have significantly higher levels of Mg and K, the levels are below those normally considered to be toxic to most plant functions (Epstein 1972; Brooks 1987). The higher Ca/Mg levels and higher pH of the var. *sceptrum*-occupied outcrops may be explained by the intercalation of the silicic volcanic ashes throughout the oolitic calcareous deposits characterizing the more southeastern part of the western Snake River Plain. Indeed, some of the var. *sceptrum*-occupied outcrops (HC and CC in Table 3, most notably) had much higher levels of Ca than other sites tested. Although Izett (1981) has demonstrated that the ash falls throughout this region are of varying origins and compositions, no detailed mapping of the outcrops occupied by any of the *E. calcareum* populations has been performed. Regardless of whether the variation in substrates of the two varieties of *E. calcareum* originated from differing source materials or subsequent processes that these geologic units may have undergone, or both, the important point is that the morphologically and geographically distinguishable varieties occupy soils of significantly different chemistry (Table 4).

The biological significance of these chemical differences among the outcrops occupied by *E. calcareum* is not clear. It is possible that some morphological differences may result from nongenetic effects rather than adaptation. Higher Ca/Mg ratios are known to increase plant growth (stem height) experimentally in willows (Mleczek et al. 2012). The longer scapes of var. *sceptrum* (than var. *calcareum*) may result from a direct phenotypic effect of the higher Ca/Mg ratio in outcrops they occupy. Alternatively, at least some morphological differences may result from adaptation resulting from different selection pressures experienced by populations of the two different varieties. Numerous studies investigating endemism on challenging substrates, including serpentine (Jenny 1980; Kruckeberg 1985; Brooks 1987; Kruckeberg 2002; Taylor et al. 2002; Harrison and Rajakaruna 2011), gypsum (Moore et al. 2014; Escudaro et al. 2015), shales (Silva and Ayers 2016), and gabbro (Medeiros 2015) have demonstrated that extreme mineral compositions or physical soil properties can impose selection pressures on plant populations and drive significant adaptation (Rajakaruna et al. 2003; Sambatti and Rice 2006, 2007), which, in turn can stimulate speciation (Harrison et al. 2004; Brady et al. 2005; Anacker et al. 2011; Kay et al. 2011). It is possible that varietally distinct populations of *E. calcareum* studied here are likewise being subjected to significantly different edaphic environments to the extent that adaptation can occur. The levels of minerals in the outcrops occupied by *E. calcareum* are unlike those in many environments previously studied where adaptation has been demonstrated. For example, the lowest Ca/Mg ratio observed in this study (1.7; Table 4) is still within the range that normally imposes no stress to plant functions (values

> 1; Epstein 1972; Brooks 1987) and well above those levels considered chemically challenging in ultramafic soils (0.04–0.2; Brooks 1987). Levels of Ca, Mg, Na, and K in all outcrops examined in this study, while variable, are not outside of the range considered normal for plant growth (Epstein 1972). There still may be selection forces that operate differently, albeit more slowly than in ultramafic sites, in the outcrops occupied by the two varieties of *E. calcareum*. There are many components of soil chemistry and physics of these outcrops that have not been studied yet.

While differential edaphic selection may be low between the varieties, the barren nature of the ash outcrops throughout southwestern Idaho and southeastern Oregon, including those occupied by *E. calcareum*, may increase the likelihood of selection. Sambatti and Rice (2006) have demonstrated in ultramafic sites that local adaptation is only evident in the absence of competition, so the low cover of vascular plants evident in these ash outcrops may contribute to more rapid selection. And although the particular stressors to vascular plants in the ash beds of this region have not been ascertained (Grimes 1987), the edaphic environments are unproductive and, as such, minimize competition (Harrison and Rajakaruna 2011).

Some of the morphological differentiation seen in *E. calcareum* (Table 3) may result from isolation of the varieties from one another. Insofar as isolation reduces gene flow (Futuyma 1997), the patchy, isolated nature of the barren outcrops occupied by *E. calcareum* can enhance genetic differentiation of varieties. Distances between the varieties on either side of the western Snake River Plain are greater than those from one outcrop to another within the range of each variety. That is, the outcrops in the northwestern end of the range (those occupied by var. *calcareum*) are no closer than 84 km from the closest outcrops in the southeastern part of the range (those occupied by var. *sceptrum*—Fig. 2). Distances between adjacent *E. calcareum* var. *sceptrum*-occupied outcrops vary from approximately 1 km to no more than 50 km. And distances between adjacent *E. calcareum* var. *calcareum*-occupied outcrops range from a few hundred m to no more than 50 km. Though there may be populations of *E. calcareum* on unexplored outcrops in either the southeastern (var. *sceptrum* range) or northwestern (var. *calcareum* range) regions of the species' range, there are no outcrops in the Quaternary sediments of the now heavily developed region of the Treasure Valley between these two sets of populations. Thus, the spatial distribution of substrates likely contributes to the differentiation of varieties in *E. calcareum*, regardless of the strength of selection. However, the importance of geographic separation and its effect on gene flow relative to selection and adaptation or other factors that may contribute to varietal differentiation cannot be adequately assessed here without evaluating genetic interchange or pollinator interaction.

The genus *Eriogonum* is one of the most diverse plant genera in western North America, and it is considered to be rapidly evolving (Reveal 2005). Many of the approximately 250 species of *Eriogonum* are narrowly restricted to specific substrates (Reveal 2005). In *E. calcareum* the geographic separation of patchy outcrops of chemically distinct substrates contributes to evident morphological differentiation of varieties.

For recently evolving populations, such as *Eriogonum calcareum* var. *calcareum* and var. *sceptrum*, geographic separation and variations in soil chemistry are likely modifying the rate of natural selection and morphological differentiation within the species. These two varieties offer an example of the ecological and geographic differentiation between plant populations of a rapidly evolving genus in North America. This study also demonstrates the potential of the archipelago of edaphic islands in southwestern Idaho and southeastern Oregon as a laboratory for the study of vascular plant evolution.

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